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THE FUNCTIONS OF THE SPIRACLE OF THE SKATE

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In the latter part of September, 1904, I spent a few days at the Woods Hole laboratory of the United States Bureau of Fisheries for the purpose of making a study of certain blood vessels of the skate. At that late season the Fisheries laboratory had abandoned its fish traps and I was supplied with material through kindness of officials of the Marine Biological Laboratory, which was still maintaining a trap in Vineyard Sound. One afternoon this trap was hauled and some seven or eight common skates (Raja erinacea) were taken. The skates were thrown with numerous other fish into the bottom of a skiff which was towed back to the laboratory by the steam launch,— a distance of about a mile. Arrived at the laboratory, I picked out the skates and threw them into a large shallow tank for the purpose of washing from them the sand and debris which had become attached to them in transit. In view of the fact that the fish had been out of the water nearly an hour and had been subjected to no very careful treatment, it did not occur to me but that they were dead, or at least beyond the possibility of reviving. By means of a hose I turned upon them a copious stream of cold sea water and then I noticed, for the first time, that feeble respiratory motions were in progress. As I continued to play the water over the fish the respiratory motions became stronger. Shortly one skate slid over the opening of the

outlet of the tank, closing it, and in a few moments a half inch of water had accumulated over the bottom of the tank. Thereupon the skates set up an energetic spouting of water from the spiracles, - a mode of behavior which had never before come to my notice. At frequent intervals a large stream of water was ejected from each spiracle, rising vertically to a height of one or two inches. (The fish were of uniform size,— about a foot in width across the pectoral fins.) The animals were not submerged, it should be remembered, but were less than half covered with water, most of the dorsal surface, including the spiracular region, being well out. The vigor and frequency of the spouting and the fact that so many skates were doing it at the same time produced an effect striking enough to compel attention. No doubt this behavior has been observed previously by others. A "Spritzloch" is certainly a spout-hole. But I could recall having met only the briefest reference to the use of the elasmobranch spiracle in respiration, so I postponed the fate of some of the skates and placed them in an aquarium supplied with running sea water, with a view to watching their respiratory movements. During the next few days I observed the fish as I could, but other work had precedence, so that I was unable to carry on any systematic study of their behavior. However, my impromptu experiments brought to light one or two facts which seem to me worthy of mention.

As must be well known, the modified first visceral cleft (spiracle) serves in the skate chiefly as an incurrent opening for the respiratory stream. So far as this function is concerned, as pointed out by Garman ('74), the spiracle is probably of greater importance in the rays than in the sharks, owing to the fact that the rays, for the most part, lie flat upon the bottom of the sea, and this habit places the mouth at a disadvantage as an incurrent respiratory opening, while in the perpetually roving sharks such is not the case. These facts are very likely connected with the fact that the spiracles occur as large openings in all the rays while in many of the sharks they are either very small or completely closed.

Many writers make the statement that water may pass either into or out from the mouth by way of the spiracle. Garman ('74) notes that, whereas the sting-rays have in the spiracular passage a valvular fold preventing outflow, in the common skate no such

structure is present, so that water may pass either way. Duméril ('65–70, tome 1, p. 210) states that water usually enters the mouth through the spiracle, but less frequently passes in the reverse direction.

While at rest on the bottom of an aquarium, the skate slightly elevates the head above the surface of the bottom in the manner described in Brehm's Thierleben (Brehm, '79, p. 387), which may well be quoted: "Abweichend von anderen Bodenfischen liegen sie mit dem Vordertheile ihres Leibes niemals fest auf, sondern stützen sich so auf ihre Brustflossen, dass in der Mitte ein Hohlraum bleibt." Continuing, Brehm's account says, "Um die Kiemen mit Wasser zu versorgen, öffnen sie ihre Athemlöcher, indem sie den Kolben zurückziehen, füllen die Kiemensäcke, schliessen die Athemlöcher und treiben das verbrauchte Wasser durch die Kiemenspalten nach aussen." According to my observations the skate takes in water not only by the spiracle but also through the mouth, although considerably more water enters through the spiracle than through the mouth.

When fully open the external aperture of the spiracle in the common skate is nearly elliptical in outline, but the curvature of its anterior margin is much greater than that of its posterior margin. The anterior lip of the opening bears the rudimentary gill and the closing of the spiracle is effected mainly by the contraction of this gilled lip, while the posterior lip, being nearly straight when relaxed, contracts but little.

In ordinary respiration the spiracle opens and closes with pendulum-like regularity. During one of the prolonged resting periods of the fish, the interval between successive openings is longer than when the fish is active, and the spiracle is not opened wide,—indeed, the opening may be only a narrow slit. During more active respiration the anterior lip of the spiracle moves back and forth with a quick decisive motion and the spiracle is opened to its utmost width. As the spiracular valve opens, the branchial region is expanded and a strong current of water is drawn in through the spiracle, the external branchial apertures meanwhile being tightly closed. At the same time that the spiracle is open, the mouth also is opened more or less and a certain quantity of water enters. I satisfied myself as to the inward current at the mouth

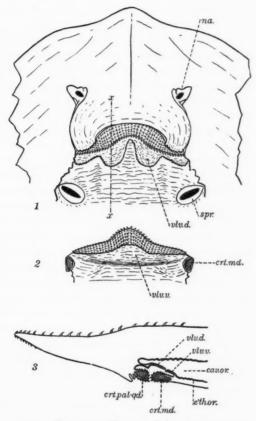
by watching the movement of solid particles suspended in the water in the vicinity of the mouth. Much the greater volume of water, however, appears to enter through the spiracle.¹ During an expiration the spiracle is shut, while the mouth tends to close but does not close tightly. The mouth action was always a little sluggish as compared with the action of the spiracle, especially in opening. As nearly as I could determine, mouth and spiracle closed together, but the opening of the mouth was slightly later than that of the spiracle. As spiracle and mouth close, the branchial region is contracted and the water contained in the gill chambers is forced out through the gill clefts.

That water does not flow out through the mouth as well as through the gill clefts during an expiration is probably due to the action of a well developed respiratory valve similar to those described for teleosts by Dahlgren ('99). The dorsal flap of the valve (Figures 1 and 3, vlv. d.) is a conspicuous bilobed fold of the oral membrane, while the ventral or mandibular flap — a less extensive fold — is broadest in the median region of the lower jaw and becomes much narrower towards the sides of the mouth. Judging from the relative widths and the positions of the two parts of the valve, it appears that the prevention of outflow through the mouth must depend mainly upon the action of the dorsal flap. Garman ('74) mentions only the dorsal one of these two folds.

The elevation of the forward end of the fish above the surface on which it rests would seem to facilitate the respiratory process.

¹ To observe these respiratory movements I put a fish in a large rectangular flat-bottomed glass vessel. The vessel was placed upon a high table so that one end projected some distance beyond the edge of the table. The fish was an object held just underneath the mouth could be seen directly through the head of the fish by looking, at the proper angle, into the spiracle as it opened, and, similarly, an object held just above the spiracle could be seen by looking upward into the mouth as it opened. This was sufficient proof that mouth and spiracle were open at the same time. In order to see the dorsal and ventral surfaces of the head at the same time so that the action of spiracle, mouth and gill clefts could be observed simultaneously. I viewed the spiracle by total reflection from the surface of the water. Having the water at a certain depth and looking upward from underneath the overhanging vessel at just the proper angle, I could see by reflection the dorsal surface of the head with sufficient clearness, while at the same time I had a direct view of the ventral surface of the head.

Is the spiracular current ever reversed — that is, does the spouting occur — in normal respiration? To answer this question



RESPIRATORY VALVE OF Raja erinacea.

Fig. 1.— Ventral aspect of the head of a skate, the lower jaw and floor of mouth having been removed so as to show the roof of the mouth and the dorsal flap of the respiratory valve (vlv. d.). na., nostril; spr., oral aperture of spiracle. Fig. 2.— Lower jaw and anterior part of floor of mouth, showing the ventral or mandibular flap of the respiratory valve (vlv. v.). crl. md., cut end of mandi-

bular cartilage.

Fig. 3.— Parasagittal section of the jaws at the position of the line xx, Figure

1. cav. or., mouth cavity; crt. md., mandibular cartilage; crt. pal-qd., palato-quadrate cartilage; e'th. or., oral epithelium; vlv. d., dorsal flap, and vlv. v., ventral flap, of respiratory valve.

I watched the respiration of skates in aquaria supplied with running water, observing the fish at times when they had not been disturbed in any way for several hours. At such times the rate of respiration was always slow,— usually from 22 to 30 inspirations per minute. At fairly regular but long intervals there occurred a break in the regular alternation of inspiration and expiration. This break was brought about in the following way. Immediately after an inspiration (and therefore in a period ordinarily marked by a contraction of the pharynx with closed spiracle and open gill clefts) the spiracle remained open and the gill clefts remained tightly closed while a particularly vigorous contraction of the pharynx caused the contained water to be ejected forcibly from the spiracle. It is apparently by muscular action that the gills are kept closed during the spouting, since the pressure of the water in the gill chambers would tend to force open the external valves. During the spouting the mouth was open, as it is during inspiration, and some water escaped from it, but very little as compared with the amount ejected from the spiracle. It is doubtless due to the respiratory valve that the outflow from the mouth is not greater. The contraction which caused the spouting was immediately followed by an expansion of the pharynx, the spiracle still remaining open and the gill clefts closed, and respiration then proceeded in the usual way. In animals which had been at rest for several hours, the rate of respiration being then at its lowest, the spouting occurred at intervals of five to ten minutes.

Having found that spouting is a feature of normal respiration in a resting fish, I next sought to discover what part the spouting plays in the respiratory process. With this end in view, I observed the fish under other conditions than rest.

Effects of Exercise.— The rate of respiration in a fish varies with the degree of activity. To induce rapid respiration I caused the fish to take exercise. This was effectively done by grasping and holding the skate firmly by the tail. The most violent efforts are made to swim away from the detaining grasp. Following are accounts of several experiments in which the rate of respiration was caused to vary.

(1) A skate had been undisturbed over night in an aquarium supplied with running sea water. When first observed in the

morning the fish was at rest, the respiration being very slow and the spouting infrequent, as described above for the resting condition. I have no record of the precise rates in this case. The fish was then exercised and immediately removed to a shallow tray of water for easier observation. The rate of respiration was markedly increased, rising to 47 inspirations per minute, and a spouting occurred on the average after every nineteenth inspiration, that is, a little oftener than twice a minute. This average was obtained by counting the number of inspirations within a period covered by eleven successive spouts. The actual number of inspirations between two successive spouts varied from 15 to 23.

In a similar case the rate of respiration while at rest was 22 inspirations per minute, with spouting at intervals of several minutes. After exercise the rate of respiration was 39.5 per minute, with a spouting after every seventeenth inspiration, or at the rate of 2.3 spouts per minute.

(2) A skate which had been undisturbed, so far as I know, for two days was found resting quietly against the side of the aquarium. The rate of respiration and the frequency of spouting were determined. Then the fish was exercised vigorously for five minutes, after which it was given five minutes to become quiet so that observations could be made. Following are the results of the experiment.

	No. of Inspirations per Minute	No. of Inspirations between Spouts	No. of Spoutings per Minute ¹
Resting	30	246	0.12
After exercise	47.5	67	0.71
Increase	58%		500%

(3) A skate which had been under experiment was allowed to rest for about an hour. At the end of that time the rates of respiration and spouting were determined. Then during the next half hour the fish was subjected to some annoyance by irritation

¹ The rate of spouting is thus expressed for the sake of ready comparison with the rate of respiration (first column). Thus, a spouting rate of 0.12 means that the spouting occurred at intervals of about eight minutes.

of the spiracle and neighboring parts (see page 299). After these experiments the fish was exercised vigorously for a minute or so, after which the rates were again observed. Following are the results of the experiment.

	No. of Inspirations per Minute	No. of Inspirations between Spouts	No. of Spoutings per Minute
Immediately after one hour's rest After a half hour's annoyance, fol-	47	55	0.85
lowed by brief violent exercise, Increase	$63 \\ 34\%$	42 .	1.5 77%

The high respiratory rate (47) immediately after the hour's rest apparently means that the fish had not recovered from the effects of the experiments which preceded that hour, a rate as high as 57 having been induced in the course of these experiments.

(4) In a skate immediately after exercise, conditions were as shown in the following table.

	No of	No. of	No. of
	Inspirations	Inspirations	Spoutings
	per	between	per
	Minute	Spouts	Minute
(a)	49.5	49	1.0

This skate was then left undisturbed about three hours in a small vessel of water, which was not changed during that time. At the end of the three hours the rates were as follows.

	No. of Inspirations per Minute	No. of Inspirations between Spouts	No. of Spoutings per Minute	
(b)	39	78	0.5	
Decrease in rates, compar-				
ing (b) with (a)	21%		50%	

Immediately after the record (b) was obtained, the fish was exercised and put into well aerated water. After five minutes (to allow the fish to become quiet enough for observation) the conditions were:—

	No. of Inspirations	No. of Inspirations	No. of Spoutings	
	per Minute	between Spouts	per Minute	
(c)	49	22.5	2.2	
Increase in rates, con	mparing			
(c) with (b)	26%		340%	

In this experiment the rates of respiration and spouting are influenced by two factors, exercise and the quality of the water, and the effects of these two factors can not be separated in the results. The experiment is cited because it shows strikingly, and in accord with other experiments, that, as the rate of respiration rises and falls, the rate of spouting likewise rises and falls, but in much greater proportion.

(5) Another observation shows the effect of quiescence. A skate immediately after exercise breathed 40 times per minute and spouted twice per minute. After three hours' quiescence (during the first hour of which the fish was extremely restless), the frequency of breathing had decreased 44%, while the frequency of spouting had decreased 68%.

In several other experiments similar to those just described the same general results were obtained. Fish which had been resting quietly for several hours were found to breathe from 22 to 30 times per minute, while the spouting occurred at intervals of several minutes. After vigorous exercise the frequency of breathing was always increased to a rate between 40 and 60 per minute and the spouting occurred once per minute or oftener. Thus, when the rate of respiration becomes more rapid as the result of exercise following a period of rest, the frequency of spouting is increased also, but in much greater proportion. A very rough average, from all of the observations taken together, shows that, whereas the rate of respiration is increased about 100%, the rate of spouting is increased at least 500%.

With quiescence, the rates of respiration and spouting drop towards the low resting rates, but the spouting rate falls off relatively much more rapidly than the rate of breathing.

Effects of Partial Asphyxiation.— Is the frequency of spouting affected by partial asphyxiation? The behavior of the fish when first brought into the laboratory suggests this question. The following experiments were made.

(1) A skate was put into a rectangular glass vessel measuring about 12 by 18 inches, containing sea water to the depth of about 3 inches. The fish was allowed to become quiet and then was left undisturbed for two hours, during which time a copious stream of water was flowing into the vessel. At the end of this period the animal was found resting quietly, respiration being at the rate of 22 per minute, while spouting occurred at very irregular intervals averaging about $1\frac{1}{3}$ minutes.

The stream of running water was now shut off and the fish was left in the vessel without change of water for about three hours. During the earlier part of this time there were alternate periods of quiet and unrest. In one of the periods of quiet, the respiration was slow and the spiracle was only slightly opened. But after a minute or two of these resting conditions, respiration became markedly quickened, the spiracle being opened wide at each inspiration, and shortly the fish raised its head and began to swim about, usually trying to swim up the low vertical side of the aquarium so that the head was thrust out of the water. This activity lasted usually less than a minute, after which the fish dropped to the bottom of the aquarium and became quiet, the respiration at once slowing down to the normal resting rate. Sometimes the performance was varied in that the quickened respiration which marked the close of an interval of rest was followed, not by the swimming activity, but by a vigorous spouting, after which slow respiration was resumed. At still other times the period of unrest was marked by both the swimming and the spouting. Occasionally the spouting occurred also in the resting intervals.

During the second hour after the incurrent stream of water was shut off the alternate periods of rest and unrest continued. The rate of respiration, however, gradually increased, reaching a maximum at the end of the second hour when the fish was breathing 59 times per minute and spouting about once per minute. Respiration was equally rapid during rest and unrest. The activity was often much more violent than in the first hour of the experiment.

In the third hour of the experiment the rate of respiration diminished with increasing rapidity. Following is the record (the running water having been shut off at 1.00 P. M.).

3.00 P. M. Rate of respiration 59 per minute

3.20 " " " 57 " " 3.45 " " " 50 " " 4.00 " " " 40 " "

The spouting continued at the rate of about once per minute. The resting periods were considerably longer than in the preceding hours and the activity was less violent. The fish evidently was becoming sluggish. Returning at 4.10 to observe the fish, I found the respiration obviously much slower and rapidly diminishing in frequency. Before I could determine the rate the respiratory motions suddenly became very irregular and spasmodic and then the action of the spiracle abruptly stopped. I waited, perhaps half a minute, and then, fearing a premature end to the experiment, I turned into the aquarium a stream of water, washing it about the head of the fish. Within a minute feeble and slow respiratory movements began, shortly followed by four vigorous spoutings in rapid succession. Respiration quickly became stronger and its rate increased rapidly, reaching 48 per minute at 4.22 o'clock. The rate of spouting, at the same time, was 1.5 per minute, an increase of about 50% over the rate at 4.00 o'clock.

At 4.29 the fish was taken out of the water and left lying on the table top. For several minutes it struggled vigorously, but at the end of eight minutes the respiratory motions had ceased and there was little muscular reaction anywhere—the fish was quite The heart, however, was beating strongly. Then the animal was put into well aerated sea water. At first no sign of returning activity appeared. The spiracle was wide open and motionless. I therefore began kneading the gills and directed a stream of water into the spiracle. Almost immediately very weak, slow and irregular spiracular motions began, and in the course of two minutes regular respiratory movements were in progress, although still weak and very slow. The spiracle did not close tightly, so that some water escaped from it at each expiration. This was not regarded as spouting. The action of the spiracle rapidly quickened and strengthened, and about four minutes after the fish was returned to water I began to count the rate of spouting which was then occurring frequently. The count was made through three successive minutes. During the first minute

the spouting occurred five times, while for the entire period of three minutes there were, on the average, four spoutings per minute. At the end of the three minutes the rate of respiration was found to be 41 per minute.

- (2) Following is the record of another experiment.
 - 10.00 A. M. A skate was removed from the water.
 - 11.15 A. M. Feeble respiratory motions of gill chambers and spiracles still in progress at the rate of 28 per minute. The spiracle is continuously wide open, its anterior lip contracting very slightly at each expiratory movement. The mouth is continuously shut.
 - 11.20 A. M. The skate is put into well aerated sea water.
 - 11.21 A. M. The spiracular action is stronger and weak mouth action begins.
 - 11.25 A. M. The spiracle closes completely at each expiratory movement.

	Inspirations per Minute	Inspirations between Spouts	Rate of Spouting
11.30 A. M.	35	25	1.4
11.39	41 .	39	1.0
11.47	47.5		
11.48 (The first sw	imming motions occu	rred.)	
12.12 P. M.	57	76	0.75
2.00	47	55	0.85

These experiments, then, so far as they go, indicate that, under conditions of gradual approach toward asphyxia (as when a fish is left in a small volume of unchanged water), there is for a time increasing restlessness attended by a rising rate of respiration and greater frequency of spouting. In the cases closely followed, there were, early in the experiment, alternate periods of rest with slow respiration, and periods of activity with rapid respiration and frequent spouting. This behavior suggests that, as the fish rests normally for a time, it begins to suffer discomfort because of the deterioration of the water. There ensues, then, a brief period of moving about and rapid breathing and spouting. The momentary quickening of the respiration restores comfort and the fish sinks to rest again, soon to repeat the whole performance.

Later in the experiment the rate of respiration was continuously high, with frequent spouting.

At the near approach of asphyxia the rate of respiration gradually diminishes, but spouting continues to occur with greater frequency than under normal resting conditions.

In recovery from asphyxia respiration was at first weak and slow, but during the first few minutes of the period of recovery spouting occurred with very marked frequency,— up to five times in one minute. Within the first hour or two of the period of recovery the rate of respiration gradually rose and attained a maximum far above the normal rate in a resting skate, while the rate of spouting, after the first few minutes of excessive frequency, gradually fell, as the rate of respiration became higher. But so long as respiration continued at a high rate, spouting occurred with much greater frequency than under normal resting conditions.

Spouting Induced by Tactile Stimulation. Some chance observations led me to try the effect of tactile stimulation of the skin in the vicinity of the external spiracular aperture. When the margin of the spiracle was gently touched with the end of a glass rod or with a stiff bit of eel-grass there usually resulted immediately a spouting from both spiracles at once. But a sharper stimulation, or persistent annoyance of one spiracle, often resulted in a vigorous spouting from that spiracle only. When a spouting had once been provoked by tactile stimulation, the immediate repetition of the stimulation usually failed to produce a second spouting. But after an interval of several seconds had elapsed, renewed stimulation usually brought again the spouting response.

One skate was especially lively and responded to stimulation much more promptly and energetically than the others. This animal was experimented with for a brief time in a small tank containing so little water that the external aperture of the spiracle was submerged only about an inch. A fairly vigorous prodding of the skin at the margin of the spiracle by means of the sharppointed end of a bit of glass tubing resulted, in some twelve trials, in an extremely energetic spouting from the stimulated spiracle only. This one-sided spouting was provoked first from one spiracle and then from the other, in fairly rapid succession, by rather sharp stimulation of the spiracles alternately. The column of water

was squirted from the spiracle with such energy as to rise through an inch of water and some seven or eight inches vertically upward into the air. Frequently the stimulation was followed, not only by the spouting, but by a sudden dash to another part of the tank, as if to get away from the annoyance.

Tactile stimulation of the skin in the region of the eye also usually caused spouting. A gentle touch upon the outer corneal surface of the eyeball almost invariably provoked a particularly vigorous spouting from the corresponding spiracle. Indeed, stimulation of the cornea was found to be a more certain way of provoking spouting than stimulation of the spiracle itself. The response was always immediate and definite and in nearly every instance unilateral.

I tried also the introduction of solid materials of one sort and another into the gill chambers. I first tried sand, allowing a little to sift into the spiracle when it opened for an inspiration. Sometimes a spouting resulted, but equally often, even though a considerable quantity of sand was introduced, no response whatever followed.

Experimenting in a similar way with another fish, I found in the aquarium some shreds of filmy substance of doubtful nature. They appeared like bits of sloughed-off skin. It well exemplifies the impromptu character of all of these experiments that, making trial of whatever happened to be suggested by the materials at hand, I caused some of this doubtful filmy substance to be sucked into the spiracle at an inspiration. Invariably material of this sort was promptly expelled by spouting. Often one or two inspirations intervened between the one by which the foreign material was drawn in and the spouting by which it was expelled. Usually the spouting occurred from both spiracles at once,— rarely from only the one at which the foreign material was introduced. The material was always ejected by the same spiracle at which it entered.

In the one-sided spouting the action of the unstimulated spiracle appeared to be uninterrupted. The stimulated spiracle simply remained open during one closing of the other.

Summarizing the foregoing account, it appears that the spiracle of the common skate serves chiefly as an in-take for the respiratory

stream, but at somewhat regular intervals the stream is reversed and an expiration takes place via the spiracle, which thereby becomes a spout-hole. With quickened respiration due to exercise, the spouting occurs much more frequently than in the restingfish. Also, when a skate is confined in a small volume of water which is not changed, respiration is quickened and spouting occurs much oftener than under normal resting conditions. Whether in this case the higher rate of respiration is due directly to the condition of the water, or to the activity caused by the unfavorable quality of the water, I am unable to say. M'Kendrick ('79) states that, in the presence of an insufficient supply of oxygen the fish "breathes hurriedly." Finally, spouting occurs with excessive frequency in skates which are just beginning to recover from an advanced stage of asphyxiation. What, in view of these facts, is the probable rôle of the spouting, so far as it is a respiratory act? May it not be roughly analogous to "taking a deep breath"? An occasional reversal of the respiratory stream may serve to clear out the gill chambers, resulting in a more nearly complete change of water in them. The greater frequency of the spouting when respiration is quickened, by whatever cause, and its excessive frequency in recovery from asphyxia indicate, I think, that it has some importance in the way of increasing the efficiency of the respiratory process.

Spouting in response to tactile stimulation in the vicinity of the spiracle indicates that the fish may, under natural conditions, employ the spout-hole as a means of expelling foreign solid materials from the gill chambers, or of dislodging objects from the surface of the body in the region of the spiracles and eyes. The behavior in respect to sand puzzled me at first. Skates when resting on the sea-bottom have a habit of settling themselves into the sand and washing it over their backs in such a way that sand would, apparently, be very likely to sift into the spiracles, and one might suppose that sand would be particularly irritating. But in my experiments the skates were indifferent to the introduction of considerable quantities of sand, while soft filmy materials were promptly spouted out. On further consideration, it occurred to me that sand, being a finely divided substance, would easily wash out through the gill clefts, whereas, being heavy, it could not so

readily be forced up through the spiracles. But the larger fragments of soft material (such as bits of sea-weed) are likely to be caught on the gill-rakers, tending to clog the branchial passages, and could best be dislodged and expelled by a reversal of the currents.

The prompt, vigorous, and almost unfailing response to a touch upon the cornea suggests that the fish regularly employs spouting as a means of keeping the eyes unobstructed. The external opening of the spiracle is so near the eye that a stream spurted from the spiracle would readily wash away foreign objects which settle upon the eye.

Regarding the spiracle as one of a series of visceral clefts which were primitively similar in structural relations and in function, it is evident that, serving as it does such a diversity of uses, it has come to differ from the more posterior visceral clefts quite as markedly in its function as in its structural conditions.

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A CRITICAL AND STATISTICAL STUDY OF THE DETERMINATION OF SEX, PARTICULARLY IN HUMAN OFFSPRING.¹

F. H. PIKE.

I. Introduction.

Cuénot ('99) and Strasburger (:00) summarized the evidence in favor of the heredity of sex in animals and plants, respectively. Rauber (:00) in the same year as Strasburger, declared for the heredity of sex in man.

Bateson in 1902 suggested that the Mendelian law might apply to the heredity of sex. Castle (:03), accepting Cuénot's and Strasburger's views without question, formulated an hypothesis to account for the heredity of sex in accordance with Mendel's law. Weldon (:01) had already shown that Mendel's original results with cotyledon color in peas differed from the theoretical numbers by something less than the limits of error. At the time Castle's theory appeared, it occurred to me to gather statistics of births in order to determine in a similar way the probability that the actual numbers of male and female births would be the numbers demanded by the hypothesis.

II. REVIEW OF PREVIOUS WORK.

The idea that the sex of the offspring could be influenced by changing the environment of the parents or of the very young embryo has long been current. Yung's ('83) experiments on tadpoles, in which he was apparently able to control the sex by

¹ This study was begun under the direction of Professor C. H. Eigenmann of the Department of Zoology of Indiana University and was completed in the Hull Physiological Laboratory of the University of Chicago. The author desires to express his obligations to the health officers and registrars who have supplied him with statistics; to his colleagues in the Hull Laboratory for criticism of the manuscript; and to Professor Eigenmann for encouragement and assistance.

changing the nutrition, have been cited as a demonstration of this point. Statistics of human births have been judged in such a way as to lend some support to this view. A good review of this aspect of the question has been given by Geddes and Thompson (:01). The validity of such conclusions has been well discussed by Newcomb (:04), who has made a statistical inquiry into the probable causes of sex in the human subject. Newcomb concludes that the causes of sex are beyond voluntary control.

Cuénot repeated Yung's experiments on tadpoles with contrary results. Eggs from the same mother, but of different layings, gave a more constant proportion of males to females than Yung obtained. The ratio of males to females in the young (54.85%) females) did not differ materially from the ratio (61.5% females) existing among the metamorphosed tadpoles found in a state of nature in the vicinity of Nancy. Born ('81) found 52 per cent of females in the metamorphosed tadpoles near Breslau. Griesheim ('81) found 63.63 per cent of females in young Rana temporaria in the vicinity of Bonn. Pflüger ('81) found 64.5 per cent of females in the same vicinity, and 86.8 per cent near Utrecht. The percentage of old females in the latter vicinity he found to be 51.2. Pflüger concluded that the sex was determined in the egg. From his results on tadpoles and other animals, Cuénot likewise concluded that sex was not influenced by the conditions of development. He decided further that there was a certain sexual ratio common to the frogs of any particular vicinity, and that this ratio might vary among frogs of different localities. In view of the comparatively small number of frogs observed, the last conclusion may possibly be open to question.

Von Malsen (:06) and Issakowitsch (:06), the former for the worm *Dinophilis apatris* and the latter for Daphnia, have recently reaffirmed the statement that an abundance of food and a low temperature cause a greater number of eggs to develop into females, while a higher temperature and a scarcity of food result in the development of a greater number of males. The food supply, according to them, is the main factor in this process, and the temperature acts only indirectly by influencing the nutrition. It is to be remembered, however, that in experiments dealing with a whole animal, it is difficult to exclude all causes except food and temperature.

Strasburger (:00) made many experiments with diœcious plants, growing them on various kinds of soil and under various conditions, in the attempt to modify the sexual ratio. The following results with *Melandrium album* may be cited as an example:

TABLE I.

			Females
Kind of soil	Males	Females	to 100 males.
Fertilized garden soil	410	562	137.0
Unfertilized garden soil	235	282	120.0
Fertilized field soil	384	479	124.4
Unfertilized field soil	254	307	120.8
Sand	321	411	128.0
		Name and Address of the Owner, when the Owner, which the	
Totals	1604	2041	Mean 127.2

Thus sexual ratios for groups of plants grown under the most diverse nutritive conditions did not differ greatly from the mean. Strasburger concluded that an arbitrary determination of sex in dioecious phanerogams has never been accomplished, and he is inclined to apply this conclusion to all plants.

Rauber (:00) studied statistically the distribution of sex in man. He found everywhere an excess of male births, but this early excess in the young was changed, because of the greater mortality of the males, to an excess of females in later life, and particularly in old age. He showed that the sexual ratio for Europe was 1000 female to 1060 male births, and that this mean ratio was fairly constant in the different parts of Europe. Reasoning on the basis that, if sex was determined by environment, the great diversity of external conditions in the different parts of Europe should cause a considerable difference in the sexual ratios for the different countries, he concluded that sex is hereditary in man.

According to Rauber, there is normally an excess of female births in horses, sheep and certain other domestic animals.

Punnett (:04a) has made a statistical study of the distribution

¹ The relative death rates per million infants of each sex, as determined from Tatham's English Life Tables is 161,036 males and 131,126 females during the first year after birth. The excess of male deaths is 29,910 per million infants of each sex, or approximately 1.57%. (Cited by Punnett, :04a, p. 265).

of male and female births in London, in order to determine whether or not the sexual ratio is affected by the nutrition of the parents. For this purpose he divides London society into three groups, following Rowntree's (:02) division of the society of York. These groups are (1) the servant keeping class, (2) the artisan class in which the family earnings are in excess of 26 shillings a week, and (3) the laboring class in which the family earnings fall below 26 shillings a week. Rowntree found that, compared with a standard dietary containing 125 grams of proteid and possessing a total energy content of 3500 calories, the first group has a dietary containing more food than is necessary for the maintenance of health; that the second class has, in general, a sufficient diet, although the family must practice strict economy in order to procure it; the third class is, as a rule, seriously underfed, the average deficiency in proteids amounting to as much as 29 per cent. Assuming that these considerations apply to London as well as to York, Punnett finds that there is either no effect upon the sexual ratio which can be attributed to parental nutrition, or, at most only a very small effect. He finds also that the statement of Düsing as to the greater proportion of males among the first born children is supported by the statistics of the English lying-in hospitals. Furthermore, mothers whose first birth occurs between the ages of nineteen and twenty-three years bear a larger proportion of males at this birth than mothers whose first birth occurs either earlier or later in life.

III. STATISTICAL DATA.

On the fundamental errors in the statistics.— Rauber (:00) has considered the errors in even the best statistics, and only a brief discussion of them will be given here. In order to compute the exact sexual ratio, it is necessary to obtain statistics of all births, both premature and full term, living or still born. The effect upon the sexual ratio of disregarding the premature and still births will be pointed out below. For purposes of heredity, homologous or duplicate twins, developed from a single ovum, and invariably of the same sex, should be counted as a single birth. The author has at hand no sufficient data upon which to base an idea of the magnitude of the error which might be intro-

duced by counting such twins as two births. Of the eighteen cases of twins and triplets considered by Wilder (:04), twelve pairs of duplicate twins were females. If such a large proportion of all duplicate twins should be females, the error introduced would be considerable, and the preponderance of male births increased. The number of cases given, however, is too small to warrant drawing conclusions as to the relative frequency of male and female duplicate twins.

The sexual ratio.— The sexual ratios for eleven European countries, as they existed sometime during the latter part of the nineteenth century, have been taken from the twenty-eighth annual report of the Massachusetts State Board of Health through the courtesy of the late Dr. Samuel W. Abbott. The figure for England from 1628 to 1642 is that given by Lexis ('92). The ratio for the United States was computed from 2,021,955 births—1,038,432 males and 983,523 females—the statistics for which were furnished by the health officers of the various states having reliable statistics of births.

TABLE II.

				17	ABLI	£ 11.				
									Nu	umber of males
	Nat	tion							to	1000 females
German	Empi	re ((1871 -	1880)						1062
Switzerla	and									1063
Austria										1067
Italy										1071
France								•		1063
Belgium										1058
Holland										1063
Denmarl	ζ.									1058
England	(mod	ern	times	. Liv	ving	birth	s only	7)		1038
England	(1628	-16	(42)							1068
Sweden										1060
Norway										1061
Massach	usetts	(18	76-18	96) st	ill b	irths i	nelud	led		1066
Massach	usetts	(18	356-18	75) li	ving	birth	s only	у.		1055
United S	tates								٠	1056
M	lean o	f al	l ratio	s						1060

A considerable increase in the sexual ratio occurs when still births are included. The sexual ratio for the city of Chicago, based upon all births reported in the years 1898 to 1902 inclusive, (141,233), is 1065. During this period 4828 males and 3554 females were prematurely or still-born. If these premature and still-births are deducted from the total number reported, the number of males to 1000 females is 1035. It becomes necessary, then, to decide whether or not still-births shall be counted. Stillbirths must be reported under penalty. Since the living children are the ones voluntarily reported, their record is not complete; but we may suppose that the parents are as apt to report a birth of one sex as of the other. The statistics of living births, therefore, in localities where birth registration is not compulsory, probably approach more nearly to the true ratio than the ratio based upon both still- and living births. If birth registration is compulsory, the ratio should be computed on a basis of all births reported. The ratio for Chicago computed on the basis of living births only is very nearly the same as the ratio for England. The ratio for Massachusetts, computed from living births only, is less than that based upon both living and still births. It is probable, therefore, that the incompleteness of the statistics is the most serious source of error.

The constancy of the sexual ratio.—An examination of the statistics shows a remarkable constancy of the sexual ratio in all parts of Europe and in the United States, for a period ranging from 1856 in Massachusetts, through 1871–1880 in the German Empire, to the year 1902 in Chicago. During these years and in the various countries, there were periods of war and peace, of famine and plenty, beside a great variety of racial and climatic conditions. Yet the greatest variation from the mean, exclusive of England, is only eleven in 1000 — a difference of one per cent.

In the same country for a period of years, the ratio is approximately constant. As an example, we may take the statistics for England (Table III) during the twelve years from 1888 to 1899, inclusive.

Table III.
(Taken from Sessional Papers of the House of Lords)

	(=	- I		Males to
Year	Total Births	Males	Females	1000 Females
1899	928646	473172	455474	1039
1898	923265	468920	454345	1032
1897	921693	469180	452513	1037
1896	915331	465660	449671	1035
1895	922291	468886	453405	1034
1894	890289	453016	437273	1036
1893	914572	465711	448861	1037
1892	897957	456622	441335	1034-5
1891	914157	465660	448497	1038
1890	869937	442070	427867	1033
1889	879868	447172	423696	1033
1888	885944	451218	434726	1037
	10,864,950	5,527,287	5,336,663	1036

It will be seen that the ratio for any one year does not differ by more than four in one thousand from the mean calculated from more than ten million births. As a further example, the sexual ratio in Massachusetts, based upon living births only, for the years 1856 to 1875 inclusive is 1059. The ratio for the years 1876 to 1896 inclusive, based upon a considerably greater number of births, is 1053. The mean for the two periods is 1055. The sexual ratio for the period in which the Civil War occurred differed by approximately one half of one per cent from the later period of peace, and by less than one half of one per cent from the mean of the two periods. If external conditions exerted any effect upon the parents in such a way as to change the sex of the offspring, the change due to such influences was not greater than one in two hundred.

Social, political and material conditions in England during the years 1628 to 1642 were vastly different from those during the years 1888 to 1899, but the difference between the sexual ratios for the two periods — 1068 to 1000, and 1036 to 1000 respectively — is not greater than the difference between the ratios for the city

of Chicago computed upon the living births only for a given period, and upon all births for the same period. It does not, therefore, appear necessary to assume with Strasburger that the sexual ratio for England has changed to any considerable extent in two hundred years.

The effect of a war upon the sexual ratio.— It has long been a current belief that more males were born in a period following a war than in a similar period of peace. Newcomb considers this statement unworthy of serious consideration. It may be said that, so far as the United States is concerned, such statements are based upon an insufficient number of births, and that the statistics are for the most part worthless. I have many letters from state health officers to the effect that there are now no reliable statistics of births in their respective states.

The sexual ratio independent of external conditions.— In view of the remarkable constancy of the sexual ratio under diverse social, political and material conditions and for long periods of time in different races, it seems incredible that the determination of sex should be dependent upon external conditions.

If the sex of the offspring is independent of external conditions, what is the determining factor? Two general explanations are open. There is first the possibility that sex is determined by a series of accidents, as Newcomb suggests, and second, the possibility that sex is hereditary.

The possibility that sex is determined by a series of accidents.—Newcomb likens the sex of a child to a particle floating on a stream of water. In the early part of its course the stream is single, but an obstacle divides it into two at the lower part. A particle entering the stream at the upper part may pass on either side of the obstacle, the exact course depending upon a multitude of accidental causes up to a certain point, after which its course on one side of the barrier or the other is fixed. So with an ovum. In its early development, there is the possibility of developing into either a male or a female, the sex depending upon a series of accidents.

Newcomb showed from statistics that the probability that twins will be of the same sex is .77, and the probability that they will be of opposite sexes is .23. It is impossible to tell from Newcomb's

tables whether duplicate twins were excluded, as they should have been, since but one ovum is involved. If duplicate twins had been excluded, the probability that ordinary twins would be of the same sex might have been even less than .77; for duplicate twins are invariably of the same sex.

Sex determined before the first cleavage of the ovum. - Let us now examine into the bearing of these considerations upon Newcomb's hypothesis. To continue his simile, two particles starting together will have a greater chance of remaining together and passing on the same side of the barrier than two particles somewhat removed from each other. Similarly, two ova developing together (in the same environment) will have a greater chance of producing offspring of the same sex than two ova developing at different times, but neither the two particles nor the two ova invariably follow the same course. If any series of accidents acting upon the ovum after fertilization is to determine the sex of the twins, it is incredible that it should always produce the same result in both. Since, however, duplicate twins are always of the same sex, this view becomes untenable, and we must limit the action of a series of accidents to the period preceding and possibly including fertilization. The conclusion that at or immediately after fertilization. the sex of the offspring is determined once for all seems inevitable. The effect upon the ovum of any series of accidents must cease before the first cleavage is accomplished.

Is sex determined by either parent alone?—Having concluded that the sex of the offspring is determined at or before the time of fertilization, we may inquire further whether the sex of the offspring may not be determined by the ovum alone, or by the spermatozoon alone. First, the ovum may have the potentiality of developing into either a male or a female embryo. During maturation the chromatic material necessary for the development of an embryo of one sex is cast off in the polar bodies, and that necessary for an embryo of the other sex is retained. The spermatozoon thus plays a purely asexual rôle. This hypothesis postulates a qualitative reduction of the chromatin in maturation. According to another variety of this hypothesis the ovum assumes the asexual rôle, and the sex of the embryo is determined solely by the spermatozoon. Since all spermatozoa do not produce

embryos of the same sex, there must have been, at some period in the development of the spermatozoon, a qualitative reduction of the chromosomes, those necessary for a male going into one spermatozoon, and those necessary for a female into another. If we accept this hypothesis, we must show why a constant and unequal proportion of all ova or of all spermatozoa have chromosomes, e. g. the accessory chromosome, which will produce an embryo of a certain sex. As an alternative hypothesis we may suppose that both ovum and spermatozoon play a sexual rôle, and that the sex of the embryo, in common with other characteristics, is determined by both sexual elements. This view, as I shall show subsequently, is the more probable.

If we cannot explain the cause of sex by postulating a series of accidents of unknown nature occurring after fertilization, can we explain it on the second possibility,—heredity? And if so, which of the two great laws of heredity are applicable to the case? The first question I shall answer in the affirmative, and proceed to the discussion of the second.

The application of Mendel's law.— On the basis of Mendel's law we must suppose that each ovum has equal chances of developing into a male or into a female embryo. Given two thousand ova, chosen at random, the chances are even that a thousand of them will develop into males and one thousand into females. We might reasonably expect also that in some groups we would find an excess of males, and in others an excess of females, but the mean of all groups would be 1000 each of males and females.

Punnett (:04b) in order to test Bateson's suggestion, attempted an enumeration of the sexes in *Carcinus mænas*. He found an excess of females in groups of individuals of the same size, but this excess decreased in groups of younger individuals and there were indications of an approximately equal distribution of the sexes at the time of hatching. The exact proportion of the sexes at the time of hatching could not, however, be determined.

McIntosh ('04,) from a study of the Norway lobster, concluded that the young were hatched in about equal proportions of the sexes, but was not able to determine the exact proportion.

Taking the English statistics given in Table III as a basis, we may compute the probability that the actual distribution of males

and females would be obtained by such a random choice. Instead of the theoretical distribution of 1000 males and 1000 females, the actual numbers of males and females in 2000 births are 1017.6 and 982.4 respectively, or, for convenience in calculation, 1018 males and 982 females. The probability that, in choosing at random, we should obtain such a distribution is $.60984 \times 10^{-920}$. The probability that in eleven such choices, we would always obtain the same distribution is infinitesimal. The probability that, in every case where the births are numerous enough to be representative of the actual conditions, we should always obtain practically the same distribution is practically zero. There is about the same probability that Mendel's law holds for all these cases.

A single concrete example taken from organic chemistry will serve to emphasize this point and perhaps to make this mathematical abstraction clearer. In the transformation of acetaldehyde to lactic acid by the addition of hydrocyanic acid, saponification and oxidation, each of two isomeric forms of lactic acid is, on the theory of probability, equally likely to be produced. The two forms differ in optical activity, one being dextro-rotatory and the other laevo-rotatory. Experimentally, it is found that the two forms are actually produced in exactly equal amounts, and the mixture of the two is optically inactive. A variation of from three to seven per cent from the theoretical yield would be fatal to the theory of probability. In general, in the synthesis of organic bodies in which two isomeric forms are possible and theoretically equally probable, the experimental results agree much more closely with the theory than do the statistical results of human births.

Neither ovum nor spermatozoon play asexual roles.—It is evident that these considerations apply also to the hypothesis that either the ovum or the spermatozoon play a purely asexual rôle. If we suppose that, in the qualitative reduction of the chromosomes, male and female chromosomes are equally likely to be extruded in the polar bodies, there is practically no probability at all that we would obtain the actual distribution of males and females. If the hypothesis is correct, there must be some definite regulative mechanism of unknown nature which determines the extrusion of the chromosomes. It is incumbent upon those

who maintain the truth of such a hypothesis to explain the nature of this unknown mechanism.

In the case of the accessory chromosome (McClung, :02), the statement is made that it occurs in one half of the spermatozoa of Orthoptera and Hemiptera. If we are to suppose that the accessory chromosome acts as a sex determinant, and that sex characters are to be treated as if they were Mendelian alternates (Wilson, '07), we should find a sexual ratio equal to unity or differing from unity by an extremely small per cent. We cannot, however, account for the determination of sex in the human subject on any basis of an equal division of spermatozoa into male and female producing sperms, unless we suppose, as Wilson concedes for the sake of argument, that sex may be modified by external conditions. The statistical evidence is strongly against this alternative. If it can be shown that the accessory chromosome occurs in the spermatozoa of a species in the same proportion as the sex to which it gives rise occurs in the young of that species, the statistical evidence in its favor will be increased. At present, there is no such evidence in its favor, as we do not know the exact sexual ratio of the species in which the accessory chromosome has been observed.

The strongest evidence known to the author in favor of the Mendelian theory of dominance in the determination of sex is that cited by Hurper (:07) in regard to plants. That the stamens should develop and the pistil be suppressed in the fungus-infected female plants of the campion is strongly suggestive of the recessiveness of the stamens under ordinary conditions.

The application of Galton's law.— To explain the remarkable constancy of the sexual ratio by Galton's law, we have only to assume that sex, in common with other physical characteristics, is inherited equally from the paternal and maternal ancestry; and to explain the preponderance of males in the present generation, we assume that in this ancestry for five or six generations back, there has been a preponderance of males. In this we are justified since there is direct statistical evidence that, for more than two hundred years, there has been an excess of male births in England. Accepting the statistics as being reasonably accurate, the accordance with Galton's law of ancestral inheritance is much closer than with Mendel's law.

IV. THE BIOLOGICAL SIGNIFICANCE OF THE SEXUAL RATIO.

Rauber, apparently taking the view that an excess of females is the normal condition, explains the present preponderance of male births in man by supposing that those tribes or families which, in primitive times, had the greatest proportion of males would possess a certain advantage in warfare and thus be enabled to overpower those in which there was a larger proportion of females. The male preponderance, once established, would be perpetuated by heredity. This ingenious explanation, does not, however, account for the excess of females among the domestic animals. What the sexual ratio was in primitive man we have no means of knowing. Neither do we know what the sexual ratio was in horses and sheep before they were domesticated. One would expect that the sexual ratio in wild animals would depend somewhat upon the mating and breeding habits of a species. In those species of birds, in which one male mates with one female for a season or for life, we might expect that the sexual ratio would be nearly unity, the excess of one sex or the other depending on which one was exposed to the greater dangers and had the less chance of growing to maturity. In herds of wild horses, cattle and bison, there are many females to one male. All but the strongest males are killed off by the others and the number of adult males is thus kept down to the needs of the herd. Those individuals which are most likely to produce males are not always the ones likely to reproduce. In the dairy industry, females are of more value than males, and it is possible, in fact more than probable, that man has unconsciously, by selection in breeding, increased the proportion of female births.

No one sexual ratio may be taken as the standard.— If sex is hereditary, we might reasonably expect that the relative numbers of male and female births in any species would be those which, after deducting the early deaths, would confer upon the species at the period of sexual maturity of its individuals the greatest advantage in the struggle for existence so far as the production of young is concerned. This would mean that the species would enjoy the maximum reproductive power, and this condition would be fulfilled when there were no superfluous, sexually mature males or females.

Let us suppose that a species possesses the maximum reproductive power when there are x males to n females, the relative magnitudes of x and n depending upon the breeding habits of the species. Let us suppose also that a males and b females die before reaching sexual maturity. The number of males born will therefore be a+x, and the number of females b+n. The sexual ratio will be $\frac{a+x}{b+n}$, or $\frac{a+x}{b+n} \times 1000$ if we wish to express the number of male births to 1000 female births.

In a monogamous species, such as the American robin, the reproductive power of the species would be at a maximum when there were equal numbers of sexually mature males and females. If the males are more likely to be killed off than the females, a would be greater than b, and the sexual ratio would be greater than unity. Surplus males or females would die off without reproducing. In a polygamous species, such as the ox, it is not necessary that there be equal numbers of sexually mature males and females to give the species its maximum reproductive power, and a + x might well be less than b + n. The sexual ratio would in this instance be less than unity. The relative proportions of the sexes in any species may, therefore, be looked upon as one of the physiological adaptations of the species, determined by the conditions of its existence.

V. THE EXPERIMENTAL POINT OF ATTACK.

If sex is inherited according to Galton's law it should be possible, by suitable selection of the parents, to establish a strain of animals or plants in which males or females occur with any desired degree of frequency compatible with perpetuation of the species. The practical benefits of the favorable results of such an experiment to the dairy and grazing interests of the country would be difficult to estimate. Castle has recently published some experiments on the effects of inbreeding, cross-breeding, and selection upon the fertility of flies (Drosophila) in which he found no marked change in the sexual ratio. Other experiments are now in progress.

There is, however, a second point of attack which is more distinctly within the province of the physiologist. As previously pointed out, it is difficult to imagine why ordinary twins should often be of different sexes while duplicate twins are invariably of the same sex if nutritive or any other conditions outside of the ovum itself are responsible for the sex of the offspring. It is perhaps conceivable that, in the case of ordinary twins, the placental circulation may be more highly developed, and the nutrition consequently better, for one twin than for the other, or that some peculiar local characteristic of the uterine wall may affect one twin more than the other. The probability of any such dissimilarity of conditions in the case of duplicate twins, where the same placenta supplies both with nutriment, and any local peculiarity of the uterine wall affects them equally, is very small. It must therefore be admitted that ordinary twins may be subjected to more diverse conditions during development than duplicate twins, and it is conceivable that the latter might sometimes be of opposite sexes if we could vary the conditions during development. This would manifestly be a matter of great difficulty in mammals, but a simpler method of attack is open.

Roux ('85) and others have shown that the individual blastomeres of a frog's egg will, when separated from the others, develop into complete embryos. Such embryos are presumably comparable in all respects to duplicate twins, and if by any means we might cause two blastomeres from the same ovum of any animal normally reproducing sexually to develop into embryos of opposite sexes, we would have a demonstration that sex was not determined at the time of fertilization of the egg. Failure to produce from the same egg two embryos of opposite sex would be evidence that we have, at present, no known means of changing the sex of the embryo after fertilization of the egg. It is incumbent upon those who maintain that sex is determined by the environment to show that two embryos of opposite sexes can be produced from the same ovum. The experimental solution of the problem of the causes which influence the sex of the offspring, as well as the significance of sex itself, is to be sought in the simple cell whose environment can be varied in a known way and to a known extent. It is obvious, also, that the problem of sex determination is but a particular phase of the much wider problem of the extent to which the ovum may be modified by a change in the external environment. Furthermore, if we acquire experimental data on the determination of sex, we will at the same time acquire experimental data on the question of a period of sexual indifference in the development of the individual. If sex is determined, as appears probable from the statistical data, at the time of fertilization, it is difficult to conceive of a period of real sexual indifference in the history of the individual. But if we can influence the sex of an individual after fertilization of the ovum, we will at the same time demonstrate a period of sexual indifference in development.

The bearing of artificial parthenogenesis on the problem of sex. - In a personal communication to the writer, Dr. Woelfel has suggested that if, by any means other than fertilization by a spermatozoon, we are able to cause an ovum of an animal which normally reproduces bisexually to develop to sexual maturity, we will have a demonstration that one parent plays a purely asexual rôle in the production of sex. This conclusion, however, does not follow necessarily. Moreover no individual arising by artificial parthenogenesis has as yet grown to sexual maturity. Whether this failure of normal development is due to improper nutrition of the young or to a lack of some essential detail in fertilization cannot, perhaps, be stated at present. One is inclined to regard the production of a sexually mature individual, which may in its turn reproduce, and the transmission of certain hereditary characteristics to the offspring as two essential details of fertilization. Until these phenomena have been imitated by artificial means, one is loath to believe that normal fertilization is imitated in all essential details by artificial parthenogenesis (Loeb:06). The study to artificial parthenogenesis may have an important bearing upon the determination of sex, but the true significance of the work already done is not apparent.

VI. SUMMARY AND CONCLUSIONS.

The statistical study of the distribution of sex in man shows that there is a slight but constant excess of male births. The greater mortality of the males leads to a preponderance of females in old age.

There are certain unavoidable errors in the statistics, the two most serious being (1) incompleteness, and (2) disregard of duplicate twins. It is not probable, however, that these errors are in such a direction as would change the sexual proportion if we could get absolutely correct statistics.

The sexual ratio is remarkably constant in widely different localities and at widely different times; in a given locality the ratio is not altered by the varying social and material conditions of the parents, as indicated by statistics.

The study of duplicate twins shows that if sex is determined by a series of accidental causes, such causes cannot be operative after the fertilization and first segmentation of the ovum.

The logical conclusion from the statistical data is that sex is hereditary. Mendel's law does not apply. The constancy of the sexual ratio for more than two hundred years may best be explained by supposing that sex follows Galton's law of ancestral inheritance.

If sex is hereditary, we may explain the significance of the sexual ratio on the basis of natural selection by supposing that the proportion of the sexes in any species is such as will give that species the maximum reproductive power at the time of sexual maturity of its individual members. The sexual ratio may be expected to vary for different species, depending upon the mating and breeding habits of any particular species. The sexual proportion may be considered as one of the physiological adaptations of a species.

The conclusions drawn from statistical data should be tested experimentally. There are two experimental points of attack: (1) Breeding experiments to determine whether the sexual proportion can be altered by selection. (2) Experiments on the separate blastomeres from one ovum to determine whether two embryos of different sexes can be reared from the same egg, and whether there is a period of sexual indifference in the development of an individual.

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CHUBS' NESTS

ALFRED W. G. WILSON

During late summer, at times of low water on almost any one of the numerous small streams tributary to the Upper Ottawa River, the passing voyageur cannot fail in having his attention drawn to curious conical piles of coarse gravel and pebbles which occur along the river shores. Locally these piles of stones are called "Chubs' Nests." The following notes are published in the hope that they may prove of interest to American Naturalists.

The accompanying plates will give a general idea of the shape and character of these heaps of stones. They are conical in form, with a circular or oval base. The volume of the gravel of which they are built will vary from a good sized wheelbarrow load to about a cart load. The individual pebbles vary in size; the great majority would readily pass through a two inch ring. In a few cases oblong pieces of schist about three inches in length were noted but their cross section would not be more than one square inch. The largest pebbles used in the construction of the heaps would weigh at least half a pound each; most of the pebbles would weigh less than four ounces each. The rock material from which the pebbles have been derived is often quite different from the rock of the immediate vicinity, showing that the pebbles have been transported some distance to their present resting place. In a number of instances it was found that the interior of the heap consists almost entirely of small pebbles less than an inch in the maximum dimension, the larger ones forming only an outer layer over the whole cone.

The dimensions of two of these heaps of stones were as follows:— No. 1. Base, length 6.5 feet, width 5 feet at one end (left of figure 1), and 4 feet at the other, height 21 inches, angular slope of the side of the cone about 48° to the vertical. This pile was built of mixed pebbles, chiefly granite and schist. (See figure 1.)

No. 2. Base, nearly circular and four feet in diameter, height 22 inches, angular slope 49° 45′. (See figure 2.)

In a very large number of cases examined the stones were found to be piled quite loosely so that the slightest jar set them sliding down into a position of more stable equlibrium.

Along the larger streams and rivers the heaps are usually found in small bays off the main stream or on bars and ridges on the sides of the main channel, in quiet but never in dead water. In some places near the watersheds they occur in midstream, and occasionally they are sufficiently numerous to hinder and partly obstruct canoe navigation, where the water is shallow and the stream narrow.



Fig. 1.

In the early spring when the waters are high and usually more or less turbid the cones are not in sight; but as the waters recede the apices of the cones gradually appear above the surface and late in the season the water may have receded so that the whole cone together with the bar on which it was built comes into view. The tops of the "nests" shown in figures 2 and 3 were fully five feet above the surface of the water when the pictures were taken in August. In early June the water was probably six feet higher and the tops would have been under at least a foot of water.

As to the origin of these curious heaps of pebbles, the Indians

and Bushmen all attribute them to small fish — called *Chub* by the whites and *Awadosi* (stone carriers) by the Indians.¹ Personally I have made numerous inquiries but I have not been able to find any one who will say he has actually seen the fish at work, still they all insist that it is the fish who make them. A careful examination of over one hundred heaps, scattered along a line of gravel more than three hundred miles in length has convinced the writer that the cones are of animal origin, that the materials have been assembled by some intelligent agent, not by stream action.



Fig. 2.

These heaps of stones are said to be built in the early spring and are presumably used for spawning purposes. They are always in places where the water is smooth but still flowing. Except in the very beds of the rivers of this north country, pebble and gravel beds and bars are not found. The shores of the streams are almost universally clay. At high water the rivers expand and invade the woods so that, as one of my canoemen expressed it "The pike go into the bush to hunt." In midstream the water is usually flowing very swiftly at high water and along

¹ Bell. Robert. Recent Explorations to the South of Hudson Bay. The Geographical Journal, July, 1897, p. 16.

the shores the ground is covered with logs and bushes. Ground suitable for spawning covered by a moderate depth of water is rare. In nearly every case where the nests were seen the bottom consisted either of large boulders and cobbles, or of soft materials and sand with a certain admixture of partly decayed logs and lower types of plant life, chiefly algæ. On this bottom the conical heaps of stones were built up. It seems not unnatural to suppose that they serve the dual purpose of offering a clean gravel surface for the deposition of the eggs, and at the same time raise these eggs nearer the surface of the water and thus into a zone of more



Fig. 3.

light and warmth than if they were deposited directly upon the bottom.

The fish which are said to be the architects of these curious nests vary in size up to about 18 inches in length, and in weight up to about two pounds or a little over. Their ventral aspect is white, the dorsal dark gray-black, and the broad sides are silver white. The cycloid scales are large and thick, and the body is about three times as deep as wide. The third plate shows a specimen about 14 inches in length which was captured and laid upon the nest before making the picture. President David S. Jordan to whom these data have been submitted considers that

the fish is "probably the Silver Chub or Fall Fish, Semnotilus corporalis Mitchell." .It may be interesting to sportsmen to know that the fish rise readily to the fly, occasionally can be caught with a troll, and are easily captured with an ordinary hook baited with a piece of bacon rind. The flesh is coarse and the bones are few and large, reminding one of mullet.

In 1844 Chubs' nests were found in the Magalloway River, Maine, by Dr. Jeffries Wyman. He described them to the Boston Society of Natural History (Proceedings, Vol. 1, p. 196) as "mounds of pebbles, two or three feet in diameter, which he was told were heaped up by a fish called the Chub, at its breeding season, and that its eggs were deposited among the stones." He referred to a similar habit attributed to the lamprey eel and remarked that he was not aware of any other instance of the kind. Dr. Robert Bell, in the report of his explorations referred to above, has published a figure of a characteristic nest. He states that a varying number of chubs work together in building a mound, bringing the stones in their mouths, one at a time, from far and near.

In considering the relative sizes of the pebbles and the fish that move them, it must be remembered that under water the weight of the stones will be from one quarter to one third less than the weight in air. In the cases of the larger heaps of stones it is often found that there is an area greater than the base of the cone over which the stones are scattered. In one case we found what appeared to be the base of an old cone and the inference seems to be that in the rebuilding every spring they repair the old nests, shift them at times, and utilize materials from abandoned nests to construct new ones or to enlarge the old. The larger nests are probably the work of several seasons.

MONTREAL, January, 1907

¹The nests of the lamprey are "gravel filled pockets." "The central part is usually 15 to 20 cms. deeper than the edges, so that the whole is dish-like in appearance; at the lower edge there is always a pile of stones." The stone carrying habit of the lamprey has been described by S. H. Gage, by Dean and Sumner, and by Young and Cole (American Naturalist, 1900, vol. 34, pp. 617–620). In an interesting and comprehensive account of parental care among fresh water fishes (Rep. of the Smithsonian Inst., 1905, pp. 402–531) Theodore Gill does not include either the lamprey or the chub, the former presumably not being considered a fish. The cat-fish is described as carrying stones away from its nest; no stone gatherer like the chub is mentioned.



NOTES AND LITERATURE

GENERAL BIOLOGY

Mendelism.¹ — In a well printed booklet of eighty-five $4 \times 5\frac{1}{2}$ inch pages, R. C. Punnett of Cambridge, England, has presented an admirably clear and concise account of Mendelism. After reviewing the simple and fundamental experiments of the Abbot of Brünn, the writer describes the more recent discoveries to which they have led, and in conclusion shows them to be of the highest practical and scientific importance. Although the mendelian principles of heredity are well known in America through the publications of Castle, Davenport, and others, a brief review of them as presented by Punnett may still be of interest.

It is found by experiment that when a certain pure bred tall variety of plant is crossed with a dwarf, the resulting hybrid contains both the factors for tallness and shortness. If A represents the tall factor of one parent and a the short factor of the other the hybrid which contains both is Aa. It is not of medium height, but is like its tall parent. A character such as tallness in peas which is retained by the hybrid is called *dominant*: one like dwarfness which is latent in the hybrid is named recessive.

When hybrids Aa are bred together, they produce in the next generation 25% of pure tall forms, AA; 50% of tall hybrids, Aa; and 25% of dwarfs, aa. The familiar formula may be written thus:

Parents .	AA	aa
1st generation	Aa	
2nd generation	\overline{AA} 2 \overline{A}	1a aa

The tall hybrids Aa, and the pure tall plants AA, are indistinguishable except by further breeding. Then it appears that one in every three contains only the factors for tallness. Such plants, like the dwarfs, breed as true as if derived from an unbroken ancestry of pure forms.

It is not always the case that the hybrid resembles one of its parents.

 $^{^1\,{\}rm Punnett},~{\rm R.}$ C. Mendelism. Second Edition. Cambridge, MacMillan and Bowes, 1907. 16mo. vii + 85 pp.

The blue Andalusian fowl is a race which in breeding produces 25% of black offspring, 50% of blue, and 25% of white splashed with black. It is evident from these proportions that the blue race desired by fanciers is essentially mongrel, and can never be made to breed true. The black race and the splashed whites remain true when each is mated with its own kind, but when crossed they produce the blue Andalusian.

The fixed proportion of pure and mongrel forms in the offspring of hybrids may be readily explained. The factors A and a, derived by the hybrid from its parents respectively, are transmitted through its germ cells in equal abundance. The factors become segregated, so that one half of the germ cells contains only A, and the other half a. In the process of fertilization an A will unite with a as often as with A; and an a will join A as often as a. Thus there will be a and a for each aa and a.

When two different inheritable factors occur in each parent the number of combinations in the offspring is much greater. Mendel found, with peas, that the height of the plant (tall or dwarf) and the color of the seeds (green or yellow) were transmitted independently of one another. A and B may represent respectively the factors for tallness and greenness which are dominant; a and b the factors for shortness and yellowness which are recessive. If a tall green-seeded plant AB, is crossed with a dwarf yellow ab, tall green-seeded hybrids containing the factors AaBb result. Every germ cell of such a hybrid contains one factor for height and one for color; they are equally distributed in the four possible combinations AB, Ab, aB, and ab. When such a group of germ cells fertilizes a similar group, the following combinations are to be expected:

AA BB	AA bb	aa BB	aa bb
2AA Bb	$2Aa\ bb$	$2aa \ Bb$	
2Aa BB			
4Aa Bb			

Thus among sixteen individuals nine contain both dominant factors and in the case of the peas are tall green-seeded plants. Three contain only the dominant A, and are tall yellow-seeded forms; three contain only the dominant B and are green-seeded dwarfs. One contains neither dominant and is a yellow-seeded dwarf. This ratio, 9:3:3:1 Mendel verified by experiment.

The sweet pea known as the 'Painted Lady' has a bright pink color due to its sap, and this is dominant over the absence of such sap color

in which case the flower is white. In the cream sweet pea there is no sap color, the tint being due to pigmented chromoplasts. The yellow chromoplasts are recessive to colorless ones. Therefore when a Painted Lady is crossed with a cream, the hybrids are all Painted Ladies; in the next generation four classes are found,—Painted Ladies, cream Painted Ladies, whites, and creams, in the proportion 9:3:3:1.

A similar result has been observed in breeding fowls. The rose comb of the Wyandotte type and the pea comb of the Indian game are both dominant over the single comb of the Leghorn type. When a rose comb is crossed with a pea comb a new type results, described as the "walnut" comb. It resembles that of the Malay breed. When such hybrids are bred together four types of comb appear in the next generation, namely the walnut, rose, pea, and single in the proportion of 9:3:3:1.

In rabbits the gray color of the wild animal is dominant over albinism. When a gray is crossed with an albino, gray hybrids result which produce young in the proportion of 9 grays, 3 blacks, and 4 whites. The factors involved are pigmentation, A, dominant over albinism, a; and grayness, B, dominant over blackness, b. The four white animals which appear identical include three forms, namely aa BB, 2 aa Bb, and aa bb, all of which lack the pigmentation factor A. From this it appears that the wild gray color consists of a factor for pigmentation and another for grayness. By loss of the former a white rabbit results, and by loss of the latter, a black one. In the offspring of such a white and black, reversion occurs to the original gray form. Similarly white pea blossoms may each contain one of the two factors for pigmentation, and by crossing such whites, reversion to a wild colored type has been observed. Thus reversion has been defined as a union of complementary factors which have become separated in the course of phylogenetic development.

From these and many other observations, the author concludes that no horticulturalist can propose to raise a tall pea from a dwarf by a process of manuring, nor by selecting minute fluctuations, but only by obtaining new aggregations of unit characters through breeding. He infers that "education is to man what manure is to the pea."

—"Permanent progress is a question of breeding rather than of hygiene and pedagogics" for "the creature is not made but born."

In Mr. Punnett's book no reference is made to 'mixed inheritance' whereby the parental characters are blended in the offspring. It must be remembered, however, that rabbits with ears of medium length are obtained by crossing short-eared with lop-eared forms; and that the

crossing of some tall and dwarf plants produces those of intermediate height. The omission of such limitations may cause a student to believe that Mendelism is the universal law of inheritance.

F. T. L.

The Problem of Age, Growth, and Death.—In a series of six public lectures Professor Charles S. Minot has made known the results of his studies, now in progress, concerning the essential nature of senescence. Rejecting such criteria of old age as a halting gait or arterio-sclerosis, which pertain chiefly to man, he has sought those features which apply as well to the aged frog or fish, and even to still lower forms. Such characteristics are found in the decreasing rate of cell division, the increase of protoplasm at the expense of the nucleus, and the progressive differentiation of the protoplasm. Old age is therefore essentially a cytomorphic phase.

The rate of cell division is expressed by the "mitotic index" which is the average number of mitotic figures found, in sections, among a thousand nuclei. The mitotic index falls from 18 to 13 in rabbit embryos of 7½ and 13 days respectively. Drawings, on the same scale, of nuclei of the various tissues in rabbit embryos of 7½ to 16½ days show a striking reduction in the actual size of the nucleus, except in the case of the nervous tissue. Even there, in relation to the protoplasmic mass, the nucleus may be relatively small.

The rate of growth begins to decline before birth, and this rate of decline rapidly decreases until old age, when growth is at its minimum. The uninterrupted process of senescence was demonstrated by weighings of rabbit embryos of various ages, and of individual guinea pigs, rabbits and chickens, from birth until death. The same law was held to apply to man, both in physical development as shown by statistics of weight, and in mental development as determined by psychologists. During the first months after birth, progress in acquiring concepts of time, space, the ego, and the external world is more rapid than in later years. As with weight, the rate of decline is most abrupt at the outset, becoming gradual as age advances.

The study leads to the paradoxical conclusion that the changes of senescence are most marked in the years of infancy, for the popular idea of maximum efficiency as the mark of maturity is set aside. The embryo in adding an ounce to its weight is rated as advancing more rapidly than the child in gaining a pound; the insect which leaps many times its own length would be regarded as more successful in jumping than the mammal which can far outdistance it.

Because of the rapid early decline in the rate of development Professor Minot believes that the age of college entrance should be lowered, and that professional studies should be entered upon at a younger age. A final publication of these researches, which have extended through many years, is in preparation.

F. T. L.

The Hypothesis of Mimicry. - Dr. Franz Werner of the University of Vienna is a skeptical critic of the Mimikrylehre which he regards. as due to a rather crude anthropomorphic point of view (Biol. Centralbl., 27, pp. 174-185). He considers first the non-poisonous snakes which are supposed to have acquired a protective resemblance to the poisonous forms of other genera inhabiting the same locality. Since no snake-eating animal is known which makes a distinction between poisonous and non-poisonous forms, the latter cannot be protected by the similarity of pattern. Moreover in some cases there is reason to believe that the non-poisonous snake is the older type and that the venomous Elaps or Vipera is the "imitator." The stingless insects which deceptively resemble bees and wasps fare nobetter than the harmless snakes, for stinging forms are "not in the least protected from their natural enemies; they fall a prey to many birds as well as to lizards, frogs, toads, and spiders." Finn is cited in evidence that the poisonous Danais is as eagerly devoured in India by lizards of the genus Calotes as are its mimics. Poisonous forms which often exhibit bright warning colors "to signalize their unpalatability to enemies in good season" are not secure.

The similar patterns and colors of various snakes in a given locality may be due to similar climatic conditions and food supply, the pigments involved being physiological by-products. Color photography is invoked to account for the correspondence in color between an animal and its habitat. A physiological rather than a teleological explanation is desired. In other words, it is believed that similar causes produce both the forms which mimic and those which are imitated, and that there is no other relation between the two. From the reports of field observers the number of instances of effective mimicry has been so reduced that "as good as nothing remains." Dr. Werner believes that man alone has been seriously deceived.

F. T. L.

ZOOLOGY

Palms and Soles. - Dr. Schlaginhaufen of Dresden has written a brief description of the palms and soles of man and the apes, based upon a literature of one hundred and fourteen publications.1 The volar surface of the hand and fingers, and the plantar surface of the foot and toes are thickly covered with slender ridges, the cristae cutis, separated from one another by depressions, the sulci cutis. Along the summit of a ridge, a row of sweat glands opens. A primitive stage in the formation of the ridges is seen in the Prosimiae, which have small round elevations (insulae primariae) surrounding single sweat pores. Besides these primary islands there are larger elliptical forms on which several sweat pores may be arranged in a circle or ellipse, surrounding a central depression. These lenticular islands are due to the coalescence of primary islands radially arranged. A crista is formed by the coalescence of a linear series. The minutiae of the cristae, upon which personal identification depends, consist in the branches of the ridges, which may end blindly or anastomose; in detached ridges; and in the ridge patterns. The two principal patterns are the more or less concentric tactile figures, and the Y shaped groups called triradii.

Besides the bas-relief of cristae, palms and soles present the high relief of tactile cushions, toruli tactiles. For each extremity there are typically five digital cushions at the tips of the fingers or toes; four interdigital cushions near the metacarpo- or metatarso-phalangeal joints; and two or three proximal cushions,—a tibial and an elongated fibular, or a radial and two ulnar, one behind the other. This arrangement is typical for pentadactylous mammals and the cushions are well developed in marsupials, rodents, the insectivora and primates. Often the interdigital cushions fuse, as in the cat, and that between the thumb and fingers may be suppressed. Secondary cushions are not infrequent—such as a central cushion found in Cebus—but none occur in the anthropoid apes or in man. Cushions are accumulations of connective tissue and are not to be confounded with eminences due to underlying muscles. On the summits of the

¹ Schlaginhaufen, O. Über das Leistenrelief der Hohlhand- und Fusssohlen-Fläche der Halbaffen, Affen und Menschenrassen. Ergebn. d. Anat. u. Entw., vol. 15, pp. 628–662. Since writing this review, the editor has received the announcement of the following book. Kidd, W. The sense of touch in mammals and birds with special reference to the papillary ridges. London, A. and C. Black, 1907. Svo., 174 figs. 5s. cushions the complex tactile figures occur, and between them are the triradii and imperfectly formed cristae. The distribution of the triradii in the monkeys and various races of men has been elaborately plotted, showing among other things, the shifting which accompanies the altered function of the foot.

According to Whipple the cushions are essentially walking pads which are secondarily tactile. The cristae have been designated 'friction ridges' since they have been supposed to allow a firmer grasp. An area of furrowed skin has been found on the prehensile tail of Alouatta (Mycetes). The German writers, however, including Schlaginhaufen, regard the cushions as primarily tactile. The most highly developed pads (the digitals) are the most sensitive; the interdigitals are less sensitive; and the low tarsal and carpal cushions least of all. The sensory functions of the toruli, whether primary or secondary, have been demonstrated by various experiments with compass points.

F. T. L.

Literature of Ichthyology. In the Proceedings of the United States National Museum for 1906, (vol. XXXI) are numerous papers on fishes, most of them relating to the fauna of Japan. Jordan and Starks give an elaborate review of the Japanese flounders and soles, 60 species in all. Jordan and Herre discuss the herring-like fishes, and Jordan and Snyder the killifishes. Jordan and Starks give a record of the fishes collected by Prof. J. F. Abbott at Port Arthur, and Hugh M. Smith and Thomas E. B. Pope record the fishes obtained in Japan by Dr. Hugh M. Smith in 1903. Among these are four new genera, Tosana, Satsuma, Lysodermus, and Lambdopsetta.

Evermann and Goldsborough describe a new rock-fish, Sebastodes alexandri, from California; Evermann and Kendall, a collection of fishes from Argentina; and Evermann and Seale, a collection from the Philippines made by Major Edgar S. Mearns.

In the Proceedings of the United States National Museum for 1907, (vol. XXXII), Jordan and Starks describe a collection of fishes from Santa Catalina Island, California.

Among these are Germo macropterus, the yellow-fin Albacore, here-tofore known from Japan and Hawaii; Tetrapterus mitsukurii, the Marlin-spike fish, heretofore known from Japan; Lepidopus xantusi, known from Cape San Lucas; Chænopsis alepidota, known from the Gulf of California; and Luvarus imperialis, known from the Mediterranean. New species are Starksia holderi and Antennarius avalonis.

Otohime, a new genus of gurnards (O. hemisticta) is described in the same proceedings by Jordan and Starks, from Japan.

In the same Proceedings, Professor John O. Snyder gives a review of the Mullidæ or Surmullets of Japan.

In the Bulletin of the Bureau of Fisheries, vol. XXV, 1905 (issued 1906), are several important papers on the fish-fauna of our island possessions.

The "Fishes of Samoa" by Jordan and Seale contains a list of the species collected on the American island of Tutuila and the German island of Upolu by David Starr Jordan and Vernon Lyman Kellogg in 1902. About 500 species were obtained, 92 of them new to science. Most of the latter are small fishes taken through the use of poison (chloride of lime) in the pools of the reefs. The reef fauna of the islands of Samoa is remarkable for the number of brilliantly colored species. In this paper are twenty-six colored plates of the most strikingly colored of these small reef-fishes, noted since the days of Captain Cook. These plates are from water color sketches by Kako Morita. The origin and purpose of these brilliant hues of coral-reef fishes is one of the most difficult problems in evolution. It is to be noted that these colors are not confined to any one family, but that more than a dozen families of fishes participate in them.

With this paper is a check list of all the species, 1704 in number, now known from the region called *Oceania*, which includes Hawaii, Polynesia, Micronesia, and Melanesia. In all this region the fauna is essentially continuous, except as regards Hawaii. In this separated island group, the genera remain the same as in Polynesia, but the species as a rule are different. This difference is clearly due to the operation of isolation and segregation.

In the same paper is a valuable discussion of the Samoan names of fishes, and the root-words composing them, by Mr. W. E. Safford.

Almost simultaneous with this paper, but apparently with a few weeks priority, is a memoir "Zur Fischfauna der Samoa-Inseln" by Dr. Franz Steindachner, in the "Sitzungsberichte der Kaiserliche Akademie" (1906) in Vienna. Dr. Steindachner describes the species of fishes collected at Apia in Upolu, by Dr. Rechinger. This collection contains 120 species, of which 20 are new. Only one of the new species is contained in the series described by Jordan and Seale. This is Salarias rechingeri Steindachner, called Salarias garmani by Jordan and Seale. A new genus, Kræmeria, is added to the rare family of Trichonotidæ.

In the next volume of the Bulletin of the Bureau of Fisheries,

(XXVI), Jordan and Seale discuss the "Fishes of the Islands of Luzon and Panay" as represented in a collection made in 1900 by Dr. George A. Lung, Surgeon in the United States Navy. Dr. Lung obtained at Manila and Iloilo, 249 species, of which eighteen are described as new. One of these species, Rhinogobius lungi proves identical with an older species Rhinogobius nebulosus (Forskål), and Petroscirtes vulsus is the young of Petroscirtes eretes.

The same rich fauna is discussed in a similar paper which immediately follows the other in the same Bulletin, "Fishes of the Philippine Islands" by Evermann and Seale. This treats of the collection exhibited at the Louisiana Purchase Exhibition, most of it being obtained by Mr. Charles J. Pierson, formerly of Stanford University. In this collection are 296 species, of which 22 are new.

One of these, Platophrys palad, should have been referred to the genus Pseudorhombus of Bleeker, of which the American genus Cencylopsetta seems to be a synonym. Three other species of Pseudorhombus are by some slip of the pen referred to Platophrys. It may be noted also that Amia fasciata (white) is a species quite different from Amia novemfasciata.

Under the title of "Fishes of Australia (Sydney, 1906), Mr. David G. Stead, naturalist to the Board of Fisheries for New South Wales, gives a convenient popular account of the food-fishes of Australia, with a useful record of the vernacular names applied to them. This book is very well written, and contains much unpublished material. It should lead to a general descriptive catalogue of the vast fish-fauna of the Australian continent.

In the Bulletin of the Museum of Comparative Zoology, vol. L, 1906, Dr. Charles R. Eastman describes numerous shark's teeth and cetacean bones found in deep sea dredgings of the Albatross.

In the same bulletin (vol. XLVI, 1906), Dr. Charles H. Gilbert describes certain lantern-fishes in the Museum at Cambridge. *Dia-phus nocturnus* Poey is described and figured from the type. A new species, *Diaphus garmani*, is described from Cuba.

In the same bulletin (vol. L, 1906), L. J. Cole and Thomas Barbour describe a collection of vertebrates from Yucatan.

There are 45 fishes, Rhamdia depressa and Rhamdia sacrificii being new. Jordanella floridæ, a characteristic species of the Florida everglades, is reported from near Progreso, and the rare species, Emblemaria atlantica and Corvula sanctæ-luciæ, from the sea near the same town.

In the Anales del Museo Nacional de Buenos Aires, Dr. Fernando

Lahille describes a remarkable new genus of mackerel-like fishes from Argentina under the name of *Chænogaster holmbergi*. The dorsal and anal fins are provided with finlets; the mouth is very large, and the body is covered with large scales. An allied fish is described by Dr. Lahille from Port Lyttelton, New Zealand, under the name of *Lepidothynnus huttoni*. Both of these are regarded, probably correctly, as related to *Gasterochisma melampus* of New Zealand. Figures of all three of these species are given by Lahille.

In Volume III, of Marine Investigations of South Africa (1905), Dr. J. D. F. Gilchrist, Government Biologist of Cape Colony, describes seventeen new species of fishes found in rather deep water off the Cape of Good Hope. Several of these are most interesting additions to our knowledge of fish-forms.

The Biennial Report of the State Board of Fish Commissioners of California for 1906 contains useful accounts of the trout of California, those of the Sierras by Dr. B. W. Evermann, the others by Dr. D. S. Jordan. The report is edited by Charles A. Vogelsang.

One of the most valuable monographs of a single type of fishes is the magnificent paper entitled, "Chimeroid Fishes and Their Development," by Bashford Dean, published by the Carnegie Institution.

This paper treats especially of the anatomy and development of the California Chimæra called Rat-fish or Elephant-fish, *Chimæra colliei*, as studied in the Hopkins Seaside Laboratory at Pacific Grove in California. The paper contains a record of the other living and fossil species. The final conclusion is that the Chimæroids constitute a highly modified and specialized offshoot from the group of primitive sharks.

In the Transactions of the Zoological Society of London, 1906, Dr. G. A. Boulenger continues his papers on the fresh water fishes of Africa with a memoir on the fishes of Lake Tanganyika.

In the Proceedings of the Royal Academy of Amsterdam, Professor Max Weber discusses the fresh water fauna of New Guinea. He divides these fishes into two groups. The fluviomarine group is derived from the marine fauna of the East Indies. The fluviatile group is derived from the river fauna of Northern Australia. In his view, New Guinea was joined to Australia at a time not later than the Pliocene.

In the Biologia Centrali Americana, published in London (October, 1906), Mr. C. Tate Regan gives an account of the fresh water fishes of Mexico and Central America, a group generously represented in the British Museum. According to Regan, *Eleotris æquidens*, from

Mazatlan, is the same as Electris picta from farther south. Dormitator latifrons, of the Pacific slope, is regarded as different from Dormitator maculatus of the Atlantic. The name, Chonophorus banana, is used instead of the doubtfully identifiable Chonophorus (or Awaous) taiasica. Gobius quentheri is shown to be the same as Chonophorus transandeanus and Awaous nelsoni may be the same species. Sicydium multipunctatum is a new species from Oaxaca. Excellent figures are given of many of the species. In the Annals and Magazine of Natural History, XVIII, 1906, Mr. Regan has numerous papers on fishes. In "Descriptions of Some New Sharks in the British Museum Collection," the Japanese Orectolobus is separated from O. barbatus, as Orectolobus japonicus, and the Japanese Monkfish as Squatina nebulosa. This had, however, been earlier named Squatina japonica by Bleeker. In another paper in the Proc. Zool. Soc. London for 1906, Mr. Regan discusses the classification of the sharks and rays, proposing a new classification.

The following is Regan's arrangement of the families; Subclass Selachii,

Series 1. Trematopnea,

Order 1. Pleuropterygii (extinct)

Families, Cladoselachidæ.

Order 2. Acanthodii (extinct)

Families, Acanthoessida,

Diplacanthidæ.

Order 3. Ichthyotomi (extinct)

Families. Pleuracanthida.

Order 4. Euselachii.

Suborder, Pleurotremata,

Division, Notodanoidea.

Families, Chlamydoselachidæ,

Hexanchida.

Division, Galeoidea,

Families, Odontaspididæ,

Lamnidæ,

Orectolobidæ.

Scylliorhinida,

Carchariida.

Division, Squaloidei,

Families, Cochliodontidæ (extinct)

Hybodontidæ (extinct)

Cestraciontida.

(Heterodontidæ) Squalidæ,

Squatinidæ.

Suborder 2, Hypotrema

Division, Narcobatoidei

Family, Torpedinidæ Division, Batoidei

Families, Rhinobatida,

Raiidæ,

Dasybatid x.

Series II. Chasmatopnea,

Order, Holocephali, Family, Pyctodontida (extinct)

Squaloraiidæ (extinct)

Myriacanthidæ (extinct)

Chimarida

The principal feature of this arrangement is the grouping together of the Cestraciont and Squaloid sharks as a division corresponding to the Galeoidea. Except for the reduction of some families to a lower rank, and a few changes in names of groups, this corresponds fairly with that adopted by recent American writers.

Under Diagnoses of New Central American Fresh Water Fishes, Mr. Regan describes *Rivulus flabellicauda*, from Costa Rica, *Rivulus godmanni*, from *Guatemala*, *Pacilia salvatoris*, from San Salvador, *Xiphophorus strigatus*, from Vera Cruz and Oaxaca, *X. brevis*, from Honduras, *Agonostomus maeracanthus* and *A. salvini*, from Guatemala.

In the Anatomischer Anzeiger, Dr. Ulric Dahlgren describes the anatomy of the electric organs on the top of the head in the Electric stargazer, Astroscopus y-gracum.

These very interesting organs constitute a new type of electric organs, quite different from those of the torpedoes and other electric fishes.

In the Proceedings of the Academy of Natural Sciences of Philadelphia, Henry W. Fowler describes *Centropomus gabbi* as a new species from San Domingo, and *C. heringi*, from Surinam. He gives a list of the cold-blooded vertebrates obtained about the Florida Keys. Eighty-six species of fishes are recorded, one of them regarded as new. This is *Congrammus moorei*, which seems to the writer a species of *Dactyloscopus*, not evidently different from *Dactyloscopus tri*digitatus, found by him at Key West. In a paper on "Rare or little known Scombroids, No. 3," Mr. Fowler proposes the new subgenus *Pampanoa* for *Trachinotus glaucus*, distinguished by the falcate fins. *Stromateus brasiliensis* is described as new from Brazil, and *Psenes chapmani*, from the Sargasso Sea.

Mr. Fowler in this and other papers adopts the generic names of Klein, published about 1740, and pre-Linnæan as well as non-binomial. These names, in his view, become available, because Walbaum in 1792 reprinted them all with their diagnoses, although not adopting them or in any way reinforcing them. In the judgment of most writers, a name published before Linnæus does not acquire validity by a reprint without acceptance. This is a matter on which some definite ruling should be made.

If we adopt these names of Klein, *Psallisostomus* will replace *Lepisosteus* or *Lepidosteus*, *Brama* will replace *Abramis*, and *Glaucus Lichia*.

A review of various genera of South American Characins is given by Mr. Fowler, as also series of useful notes on fishes of Pennsylvania.

In the Bulletin of George Washington University, vol. I, 1906, Dr. Theodore Gill tells "the remarkable story of a Greek fish, the Glanis," (*Parasilurus aristotelis*). This species was known to Aristotle, but modern authors have, with a few exceptions, overlooked its existence.

In the Smithsonian Report for 1905, Dr. Theodore Gill gives an interesting review of our knowledge of "Parental Care among Fresh Water Fishes." The literature of this subject is fully discussed.

In the Zoologischer Anzeiger, Dr. L. S. Berg discusses the fishes of Lake Baikal and those of the Amur Basin. He considers Cotto-comephorus as the type of a distinct family. This is based mainly on the peculiar structure of the caudal vertebræ. The fishes of Turkestan are also listed by the same author.

In the Bulletin of the Académie Impériale des Sciences, L. Berg discusses the lampreys of the Russian Empire.

The species of *Lampetra* or river lamprey in this vast region he reduces to two, *L. fluviatilis* and *L. planeri*. To the former he refers *Lampetra aurea* of Alaska, *L. japonica* of Japan, *L. camtchatica* of Kamchatka and other nominal species.

Lampetra planeri, according to Berg, includes L. mitsukurii of Japan and L. wilderi of the Eastern United States. This last determination is certainly doubtful.

In the Proc. Zool. Soc. London, Prof. W. B. Benham and W. J. Dunbar describe the skull of a young Ribbon-fish, *Regalecus*, from New Zealand.

In the 24th Annual Report of the Fishery Board for Scotland, Dr. H. C. Williamson describes the small cod-fish, *Gadus minutus* and *Gadus esmarki*, and records two cases of hermaphroditism in the common cod-fish.

The fourth part of the Fishes of Japan by Otaki, Fujita and Higurashi appears with descriptions in English and Japanese and with excellent colored figures of the common 'Tai,' the "national fish" of Japan, (Pagrus major), of the Ayu (Plecoglosmus altivelis), next to the American Eulachon, the finest of all food-fishes, and other species of interest.

In the Zoological Series of the Field Columbian Museum, Dr. T. H. Bean publishes a catalogue of the Fishes of Bermuda. 261 species are recorded, many of the more rare forms being figured. The new species, previously described in the Proceedings of the Biological Society of Washington, vol. XIX, for 1906, are the following: Hippocampus brunneus, (= H. hudsonius Jordan & Evermann, not of DeKay), Holocentrus meeki, Eupomacentrus chrysus, Iridio decoratus, Iridio meyeri, Iridio microstomus, Cryptotomus crassiceps, Monacanthus tuckeri, Rhinogobius mowbrayi, Labrisomus lentiginosus, Antennarius verrucosus.

In the series of Occasional Papers of the Bernice Pauahi Museum at Honolulu Alvin Seale gives a list of "Fishes of the South Pacific" collected by him in the Marquesas, Tahiti, Solomon Islands, and elsewhere in the South Seas. Numerous new species are described, and illustrated in not very satisfactory fashion by photographs.

In the same series, William A. Bryan describes a few new or rare fishes from Honolulu.

In the Records of the Australian Museum, VI, 1906, Edgar R. Waite gives descriptions of Australian and Tasmanian fishes, and studies in Australian Sharks, with photographs of the egg cases of certain species.

In the Proceedings of the Biological Society of Washington, Hugh M. Smith and Alvin Seale describe a number of species from the Philippines, four species being new.

In the Bulletin of the Michigan Fish Commission, No. 8, Mr. Ellis L. Michael catalogs the fishes of Michigan, with reference to all Michigan notices of each species.

DAVID STARR JORDAN.

Nettling Hairs of the Brown-tail Moth. 1 — It is well known that

¹ Tyzzer, E. E. The pathology of the brown-tail moth dermatitis. *Journ.* of Med. Res., vol. 16, pp. 43-64.

certain barbed hairs from caterpillars of the brown-tail moth, when applied to the skin, may cause a severe inflammation. Dr. Tyzzer has found that these hairs occur over "two velvety brown spots which appear on the dorsal aspect of the fifth and sixth segments after the first molt." Similar spots are found after each succeeding molt upto the last two spring molts, when they appear on all segments from the fifth to the twelfth inclusive. At this time they occur also in relation with the lateral tubercles of the same segments, so that the caterpillar becomes much more poisonous than in its young stages. The tapering nettling hairs are inserted by their pointed ends into elevations upon the caterpillar; the barbs, which at intervals tend to encircle the hair, point outward. If these hairs, which are easily detached, are rubbed upon the skin they work their way inward, pointed end foremost. It was supposed that the irritation which followed was purely mechanical. Dr. Tyzzer has demonstrated a chemical poison in the following manner. If the hairs are placed in a drop of blood between a slide and cover glass, a modification of the red corpuscles takes place at the apex of the hair. There the rouleaux are broken up; the corpuscles shrink and become at first spiny, and then spherical. That this is not a physical phenomenon is shown by substituting hairs of similar shape from the tussock moth, when no reaction occurs. It is believed that a poisonous substance is emitted from the apex of the hair, although no pore is visible. If the hair is broken the reaction occurs about the fracture, but otherwise only at the pointed extremity. The poisonous substance is not destroyed by baking the hairs for one hour at 110° C, but is destroyed at 115°. In the latter case the hairs produce no dermatitis when applied to the skin, and no reaction in the drop of blood. The poison is insoluble in alcohol, acetone, chloroform, ether, acetic acid, and dilute hydrochloric acid. It appears, however, to dissolve in distilled water at 60° C, and a further chemical study is in progress.

In regard to animal coloration it may be noted that the caterpillars of the tussock moth, said to present 'warning colors,' have non-poisonous hairs; those of the Io moth, with a green 'protective coloration' are somewhat poisonous; and the poisonous brown-tail caterpillars have neither a warning nor a protective color. All three forms, moreover, are eaten by birds.

F. T. L.

Divided Eyes of Insects.— G. D. Shafer has studied the divided eyes in certain Odonata and Diptera ¹ and has followed the late stages.

¹ Proc. Washington Academy of Science, 8, 1907.

of their development in two species. The modifications are introduced in the nymph stage and are almost complete in the subimago, though the eyes rapidly increase in size at the time of the final molt. Shafer thinks that the two divisions of the eye are for vision in different kind of light the regions with larger elements and less dense pigmentation being available in twilight or in the darker hours.

Notes.— Dr. Lawrence E. Griffin has published in the Missouri Valley College Quarterly Bulletin, (6, No. 4, 1907) a handy guide to the dissection of the dogfish (Acanthias & Galius). Copies may be had from the author at Marshall, Missouri, at 25 cents each.

BOTANY

Winter Rest.—In a very comprehensive series of experiments, in one of which as many as 283 species were used, Dr. Walter L. Howard, of Columbia, Mo., has studied the effect of increase of temperature, narcotics, lack of light, and dehydrating agents upon plants in the resting condition. He comes to the conclusion that the resting period is due to external influences, which also determine its duration and intensity. It may be interrupted by the use of the above mentioned agents. Though the results they produce are identical, their action is different. An ample citation of literature enhances the value of this paper.

HENRI HUS.

Notes.— A quarto of 340 pages, devoted to a revision of the genus Lepidium by Thellung, has been separately issued from vol. 41 of the Neue Denkschriften der Allgem. Schweizerischen Gesellschaft f. d. Gesamten Naturwissenschaften, as a contribution from the Zürich Botanical Museum.

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¹ Howard, Walter L. Untersuchung ueber die Winterruheperiode der Pflanzen. Inaugural-dissertation, Halle, 1906. pp. 111.

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Vol. 5, no. 16 of the Bulletin of the New York Botanical Garden forms a general descriptive guide to the grounds, buildings and collections.

The Report of the Michigan Academy of Science, vol. 8, contains the following papers of botanical interest:— Kauffman, 'Unreported Michigan Fungi....'; Beal, 'A Study of Rudbeckia hirta,' and 'Some Botanical Errors Found in Agricultural and Botanical Text-Books.' Dandeno, 'A Stimulus to the Production of Cellulose and Starch,' 'A Fungus Disease of Greenhouse Lettuce,' and 'The Aerating Systems of Plant Tissues'; Pennington, 'Plant Distribution at Mud Lake'; Smith, 'Some Notes on Nodules'; and Sackett, 'The Association of Pseudomonas radicicola with Bacillus ramosus.'

W. T.

CORRESPONDENCE

Editor of the American Naturalist:

The Flying Fish problem, discussed by Lieut. Col. C. D. Durnford in the American Naturalist for February (page 65), seems to be now reduced to a question of keenness of eyesight. Do the wings or pectoral fins of this fish in flight move so swiftly that the motion cannot be seen? or do they not move at all?

The initial start of the fish on leaving the water is clearly due to the swift motion of the tail. When the tail is moving, either at the initial leap from the water, or when by skimming along the surface the tail touches the water, the wings are seen to be in rapid vibration. When the tail is free from the water, the wings are outspread fanfashion and seem to be held firmly and at rest without vibration, to be folded when the fish drops into the water. It takes strong muscles to hold the wings taut; we may admit that the fish has these; it would take stronger muscles to cause the fish to move through the flapping of the wings.

The problem is this: Does the fish flap its fins? In the view of Col. Durnford it does. In his view the vibrations are so rapid that to most observers they cannot be seen, except at the beginning or end of the flight, when the tail is in the water.

In the view of others, the wings are not flapped at all. When the fish rises from the body the tail is flapped, which flaps the body and causes the wings to vibrate up and down as the body itself is agitated.

The writer has watched many hundreds of flying fishes. His best opportunity has been in a small boat in the Santa Catalina Channel, where the largest of the known species, *Cypselurus californicus*, over a foot long, flies by the hundred in March. He is reasonably sure, so far as any man can trust his own eye, that the *wings do not move* when the fish is sailing, and that that portion of the fish's flight is on the principle of the aeroplane.

The following note was made by the writer in 1880:

"Their movements in the water are extremely rapid; the sole source of motive power is the action of the strong tail while in the water. No force is acquired while the fish is in the air. On rising from the water, the movements of the tail are continued until the whole body is out of the water. While the tail is in motion, the pectorals seem to

be in a state of rapid vibration, but this is apparent only, due to the resistance of the air to the motions of the animal. While the tail is in the water, the ventrals are folded. When the action of the tail ceases, the pectorals and ventrals are spread and held at rest. They are not used as wings, but act rather as parachutes to hold the body in the air. When the fish begins to fall, the tail touches the water, when its motion begins again, and with it the apparent motion of the pectorals. It is thus enabled to resume its flight, which it finishes with a splash. While in the air it resembles a large dragon-fly. The motion is very swift, at first in a straight line, but later deflected into a curve. The motion has no relation to the direction of the wind. When a vessel is passing through a school of these fishes, they spring up before it, moving in all directions, as grasshoppers in a meadow."

Very truly yours,

DAVID STARR JORDAN

February 23, 1907

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(Regular exchanges are not included)

Hawkes, C. The Trail to the Woods. New York, American Book Co., 1907. 12mo, 176 pp., illus. 40 cts.— Keffer, C. A. Nature Studies on the Farm. New York, American Book Co., 1907. 12mo, 154 pp., illus. 40 cts.— Le Dantec, F. Eléments de Philosophie biologique. Paris, Félix Alcan, 1907. 8vo, vi + 297 pp. 3 fr. 50.— Linville, H. R., and Kelly, H. A. A Guide for Laboratory and Field Work in Zoölogy. Boston, Ginn & Company, 1907. 12vo, vi + 104 pp., illus. 45 cts.— McPherson, W., and Henderson, W. E. Exercises in Chemistry. Boston, Ginn & Company, 1907. 12vo, xii + 69 pp., illus. 45 cts.— De Nussac, L. Les débuts d'un savant naturaliste, le prince de l'entomologie, Pierre-André Latreille, à Brive de 1762 à 1798. Paris, G.

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